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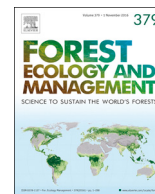
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Saproxylic beetle assemblages in recently dead Scots pines: How traits modulate species' response to forest management?

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ABSTRACT

Boreal forests have been intensively managed, influencing the spatiotemporal occurrence of dead wood, and leading to changes in saproxylic species assemblages. Some particular traits, such as habitat specialization, can be expected to make species sensitive to alterations in the amount, dynamics and heterogeneity of dead-wood habitats. We compared the saproxylic beetle assemblages of 320 dead standing Scots pines within 52 pine forest stands in three regions in Finland and Russia with contrasting forest-use history. We used the joint species distribution model of Hierarchical Modelling of Species Communities (HMSC) to analyze how the beetle communities respond to alteration of forest structure. We applied scenario simulations to examine relationships between selected species traits and environmental gradients. Our results show that tree-level characteristics were the most important variables shaping the community composition in dead standing pines, but that also the characteristics of the forest stand as well as the larger-scale landscape context affected assemblage composition. Most importantly, managed forest stands and managed forest landscapes had lost species that are specialized in their resource use. The generalist species thriving in managed forest stands and managed forest landscapes were able to utilize dead wood of small diameter and man-made dead wood types, such as cut stumps and logging residues. We conclude that forest management not only reduces the amount of resources for saproxylic beetles locally, but has also landscape-level effects so that the most vulnerable species with specialized resource use and short-lived substrates can be lost also from remnant natural forest patches embedded in managed landscapes.

1. Introduction

Forest management changes the amount, quality and spatio-temporal dynamics of dead wood and, as a consequence, saproxylic species assemblages in managed forests (Müller et al., 2008; Paillet et al., 2010). Changes in habitat structure and dynamics may favour some species, alter and impoverish species assemblages, and bias extinctions towards species with particular traits (Grove, 2002; Zavaleta et al., 2009). To assess the significance of the assemblage shift in terms of ecosystem function and species conservation, knowledge is needed on which traits are influential (Petchey and Gaston, 2002; Cadotte et al., 2011).

In boreal forests, forestry practices have reduced the overall amount of dead wood, average diameter of dead trees, amount of dead wood in advanced stages of decay, number of veteran trees and the occurrence of natural fires (Fridman and Walheim, 2000; Jonsson et al., 2016;

Niklasson and Granström, 2000). As a result of these structural changes, saproxylic species composition may shift toward species that prefer dead wood of smaller diameter and earlier decay stages and species that are generalists, i.e. species that have wide habitat niches (Gossner et al., 2013; Seibold et al., 2015; Sverdrup-Thygesen et al., 2017).

The composition of saproxylic species assemblages is influenced not only by local environmental characteristics, but also by habitat availability at larger scales (Gibb et al., 2006; Sverdrup-Thygesen et al., 2014) and the landscape context (Kouki et al., 2012). Forest stands within the same landscape share a common landscape-level history, e.g. the extent and timing of habitat loss and fragmentation, which in turn affect species persistence and their local population sizes. Some sensitive species may have gone regionally extinct and are missing from the current species pool, or they may occur only at low densities and hence are able to rarely colonize local habitats (Kouki et al., 2012; Sverdrup-Thygesen et al., 2014).

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Fig. 1. Locations of the study regions Vienansalo (Kalevalskiy National Park), Kuhmo and Pirkanmaa in Finland and Russia. The forest stands included in the study are shown by the open (natural) and filled (managed) circles.

In saproxylic beetles, several kinds of species characteristics have been recognized as potentially important to species' response to forestry practices. These include morphological (e.g. body size: [Holland et al., 2005](#); [Seibold et al., 2015](#)) and phenological traits (e.g. the flight activity season: [Gillespie et al., 2017](#)). Traits have also been used to explain species' tolerances to disturbances (e.g. decay niche: [Heikkala et al., 2016](#)). Ecological performance traits, defined as ecological requirements of a species, are combination of morphological, physiological and phenological traits ([Fountain-Jones et al., 2015](#)). They link species to the impacts of forest management on habitat conditions, particularly related to dead wood and microclimate ([Gossner et al., 2013](#); [Thorn et al., 2014](#); [Seibold et al., 2015](#)). Specialization, defined as inverse of niche width, is recognized as a fundamental trait subjecting species to extinction because of the human-induced changes either in biotic or abiotic conditions ([Clavel et al., 2011](#)). Saproxylic species confined to a certain dead wood type (e.g. fallen large logs of a certain tree species) may be more vulnerable to declining amounts of dead wood than generalist species with wider substrate requirements. In boreal Europe, examples of such species include *Pytho kolwensis* specialized on spruce logs ([Siitonen and Saaristo, 2000](#)) and *Tragosoma depsarium* specialized on large pine logs ([Wikars, 2004](#)).

The aim of this study was to analyze the influence of habitat availability on saproxylic species dwelling on recently dead standing pines (Scots pine, *Pinus sylvestris* L.) along a gradient of forest management intensity. We chose recently dead pines as the study object because it is a clearly defined and easily distinguishable host-tree type. This makes it possible to quantify the local host-tree density, and reduces the effects of host-tree quality when the aim is to compare species assemblages between different landscapes. In addition, a characteristic and species-rich beetle assemblage, including both common generalist species and several red-listed and rare specialist species, follows the

primary bark beetles in such trees.

We were especially interested in how the responses of species to forest fragmentation depend on their level of resource-use specialization. We define specialist species as those with restricted ability to use different types of dead wood as regards tree species, tree quality, diameter, and decay classes. We hypothesize that specialist species are more sensitive to changes in the quality, local and landscape-level availability of host trees than generalist species. Our particular interest is in the relative roles of habitat availability at the three spatial scales of host tree, forest stand, and landscape. Specifically, we ask: (i) Are the local saproxylic communities affected by the intensity and longevity of forest use in the surrounding landscape? (ii) Does the species assemblage depend on the local host-tree density? (iii) Do the properties of the host tree (diameter, decay stage and number of galleries made by *Tomicus* bark beetle species) affect species composition? Each *Tomicus* species is associated with its specific blue-stain (ophiostomatoid) fungi (e.g. [Kirisits 2004](#)) which may provide food to many other saproxylic beetles as well ([Stokland et al., 2012](#)) and therefore affect the communities following bark beetles. Such priority effects have been shown for other bark beetle species and later-arriving species ([Weslien et al., 2011](#)). (iv) Which traits influence the link from environmental conditions (the properties of the host trees, host-tree density, and landscape context) to species occurrence? (v) How much of the variation in the responses of species to their environment can be attributed to traits? To address these questions, we apply joint species distribution modelling to study how the beetle community and trait composition varies in relation to environmental variables measured at the three spatial scales.

2. Material and methods

2.1. Study regions and forest stand selection

We carried out the study in three study regions with divergent forest-use histories to assess the effect of landscape context. The study regions were Pirkanmaa in southwestern Finland (62°N, 24°E), Kuhmo municipality in northeastern Finland (64°N, 29°E), and Vienansalo (Kalevalskiy National Park; the former Vienansalo wilderness area) in Russian Karelia (65°N, 30°E) (Fig. 1). Pirkanmaa is characterized by a long history of intensive forest use, whereas in Kuhmo the forest-utilization history is shorter (Lilja and Kuuluvainen, 2005; Laaksonen et al., 2020). Vienansalo is located within a large wilderness area where no modern silviculture has been practiced but the forests are exposed to natural disturbance regime with low-intensity forest use in the past.

To study the effects of local habitat quality, we compared beetle communities between managed and natural stands. The studied forest stands were pine-dominated, and at least two hectares in size. The successional stage of the study stands varied from mature managed (average age of dominating trees 120–140 years, even stand structure and many cut stumps indicating previous thinnings) to natural old-growth forest (average age of dominating trees 150–230 years, no signs of previous cutting or < 10 stumps per ha originating from selective cutting some 50 to over 100 years ago), based on coring at least five dominating trees on the sample plots. The managed forest category includes also some seed-tree stands with mature pines. The fieldwork was carried out during 1998–1999 between May and September.

2.2. Environmental variables

Density of dead standing pines (diameter at breast height DBH \geq 15 cm) was inventoried on a rectangular resource-survey plot within each stand. In managed forests in Pirkanmaa, the whole stand area was inventoried because of the paucity of dead standing pines. In natural forests, the resource-survey plot was on average 2.6 ha (1.8–4.0 ha) in Vienansalo, 10.0 ha (3.0–34.0 ha) in Kuhmo, and 2.3 ha (1.8–2.7 ha) in Pirkanmaa. In managed forests, the plot was on average 9.8 ha (4.7–19.7 ha) in Kuhmo and 5.8 ha (2.0–9.4 ha) in Pirkanmaa. Within each study plot, all dead standing pines were classified according to the time since death as recently dead (died < 2 years ago) or previously dead (died \geq 2 years ago). The densities of recently and previously dead host trees were calculated per hectare.

2.3. Species survey

In each study stand, we selected randomly a total of 10–15 pines (DBH \geq 15 cm) among the trees that we found in the resource survey. In managed forests, where standing dead trees were scarce, all suitable trees were studied. All study trees had died less than three years ago. Each study tree was determined for the time since death, DBH and the number of galleries made by *Tomicus piniperda* (Linnaeus, 1758) and *Tomicus minor* (Hartig, 1834). The time since death was determined in three classes, according to whether the tree had died less than one year ago (class 1), between one and two years ago (class 2), or between two and three years ago (class 3).

To collect beetles, we set a white canvas around the root neck of the study tree. We peeled the bark with a knife and an axe for an area of 1 m² at the base of the trunk. Using standard-sized sample plots enables direct comparison of species richness and composition between individual trees. We collected all the beetle larvae and adults except larvae of bark beetles (Curculionidae, Scolytinae) for the identification. The loose bark and insect frass were sieved and inspected for any beetles later in the field or in a laboratory. Nomenclature of the beetles follows Silfverberg (2010).

2.4. Trait characterization

We compiled information on eight traits for each species (Table S1, Table S2). Traits included (1) mean body size (body length in mm); species' preferences for (2) diameter classes (diameter niche), (3) decay classes (decay niche), and (4) host-tree species; and species' preference for three host-tree qualities, namely (5) fallen trees, (6) cut stumps and (7) logging residues. We also measured species' overall specialization by summing up the number of those decay stage and diameter classes, and host-tree species (pine, spruce, deciduous trees) and dead-wood qualities (standing, fallen, cut stumps and logging residues) that are regularly used or preferred by the species. We named this trait as (8) total niche width, and it is inversely related to species' specialization level.

The realized optimum habitat for each species was calculated for two niche axes (diameter and decay stage of host tree) by applying the method presented in Appendix S3 in Gossner et al. (2013). The trait values were compiled by using information on species' habitat requirements from literature. All species traits and their calculation are presented in Supporting Information.

To account for the phylogenetic dependencies in the statistical analysis, the species were classified according to the genus, family and superfamily, using the systematic catalogue of Finnish beetles of by Silfverberg (2010).

2.5. Statistical analyses

We analyzed the data with the joint species distribution model (Warton et al., 2015) of Hierarchical Model of Species Communities (HMSC; Ovaskainen et al., 2017). As the species-level analyses are not informative for species with very sparse data, we included in these analyses only those 64 common species with at least five occurrences. At the tree level, we included as fixed effects (1) the diameter, (2) the numbers of galleries of *Tomicus piniperda* and (3) *Tomicus minor*, and (4) time since death of the tree (three levels). At the stand level, we included as fixed effects (5) the density of recently dead standing pines (measured as number of trees per hectare) and (6) the density of previously dead standing pines (measured as number of trees per hectare). As we were interested in directional differences among the three study regions e.g. due to historical or climatic differences that could not be related to the above-described variables, we included also (7) region as a fixed effect (categorical variable with three levels). To account for the hierarchical structure of the study design (trees nested within forest stands), we included the forest stand as a community-level random effect. We fitted a hurdle model, i.e. one model for presence-absence data (probit regression), and another model for abundance conditional on presence (linear regression for log-transformed count data, scaled to zero mean and unit variance within each species).

In both models, we included the following traits as predictors on how species respond to environmental variation: mean body size (log-transformed body length), host-tree preference, diameter-class preference, decay-class preference, species' use of fallen trees, cut stumps and logging residues, and total niche width.

To examine whether taxonomically related species have more similar environmental responses than can be expected based on their traits, we assumed a phylogenetically structured residual (Ovaskainen et al., 2017). As a proxy for phylogeny, we used a taxonomical tree, where we assumed equal branch lengths to the levels of superfamily, family, genus and species.

We fitted the model with the R-package Hmsc (Tikhonov et al., 2020) assuming the default prior distributions. We sampled the posterior distribution with four MCMC chains, each of which was run for 150,000 iterations, out of which the first 50,000 were removed as burn-in. The iterations were thinned by 100 to yield 1000 posterior samples per chain, and thus 4000 posterior samples in total. To explore the rate of MCMC convergence we first fitted otherwise identical models but

with 150 iterations (burn-in 50, thin 1), 1500 iterations (burn-in 500, thin 1) and 15,000 iterations (burn-in 5000, thin 10).

We examined the explanatory and predictive powers of the models through species-specific AUCs, which measure how well the model discriminates those trees at which the species occurs from those where it does not occur. To compute explanatory power, we computed the AUCs from models fitted to all data. To compute predictive power, we performed a five-fold cross validation, in which the sampling units were assigned randomly to five folds, and predictions for each fold were based on model fitted to data on the remaining four folds.

To study the independent effects of environmental variables to species richness, the occurrences of individual species, and community-weighted mean traits, we compiled gradient prediction plots (Tikhonov et al. 2020) based on the presence-absence model. We fixed the values of the non-focal variables to mode for factors and to mean for covariates. The densities of previously and recently dead standing pines were an exception because their values were highly correlated. When considering one of these as the focal variable that was varied in the prediction plot, we co-varied the other one by setting its value to the expectation conditional on the focal variable. Similarly, when we evaluated the effect of the region, we fixed the values of the non-focal variables to the most likely value within each region.

2.6. Scenario simulations

To explore how saproxylic beetle communities vary along environmental gradients, we performed scenario simulations in which we varied the environmental conditions and used the parameterized presence-absence model to generate simulated species communities (Table 1). The scenario simulations can be thought to represent potential future stand conditions, in which the density or quality of host trees may have changed because of altered management regime or effects of climate change which is expected to increase the mortality of trees (e.g. Rebetez and Dobberty, 2004; Wang et al., 2012).

First, we assumed a natural forest landscape, i.e. the Vienansalo region, as a baseline scenario (N0). In the baseline scenario we assumed that the densities of dead pines followed the mean values in the Vienansalo data (2.3 per hectare for recently and 44 per hectare for previously dead pines), and we generated data for 100 trees for which the tree-level covariates were randomly sampled from the Vienansalo data.

We defined the remaining natural forest scenarios as deviations from the baseline scenario N0. In the small-host-tree scenario (N1), we set the diameter of the host trees to the minimum value in Vienansalo data (15 cm). In the large-host-tree scenario (N2), we set the diameter to the smallest value (44 cm) that was not covered by the data of managed forests. This was done to illustrate the assemblages in large trees lacking from managed forests. In the recently-dead-host-tree scenario (N3) and the previously-dead-host-tree scenario (N4), we

assumed that time since death for all the 100 sampled pines was either less than one year ago (N3) or more than two years ago (N4). In the managed-landscape scenario (N5), we assumed the same tree and stand-level variables as in the baseline scenario (N0) but set the region to Pirkanmaa. In other words, we explored how setting a natural-like stand and its host trees into a predominantly managed landscape would affect the communities.

Second, we created a managed-forest-baseline scenario (M0) assuming a managed forest landscape with short forest-use history, i.e. the Kuhmo landscape. We sampled the tree-level covariates for 100 host trees randomly from the Kuhmo data, and assumed that the densities of dead pines followed the mean values in the Kuhmo managed-forest data (0.5 per hectare for recently and 4.2 per hectare for previously dead pines, respectively). Thus, in this scenario the stand-level habitat availability was considerably lower than in the natural-forest-baseline scenario N0.

In the high-host-tree-density scenario (M1), we assumed that the density of recently dead host trees is the mean value for natural forests in Kuhmo (1.3 per hectare) and that the density of previously dead host trees is the mean value for natural forests in Kuhmo (28 per hectare). In the long-forest-use-history scenario (M2), we kept all the tree and stand-level variables as they were in the managed-forest-baseline scenario (M0) but changed the study region from Kuhmo to Pirkanmaa. The comparison between the baseline and the long-forest-use-history scenario thus compares two forest stands that are otherwise identical but differ in the wider surrounding landscape in which they are embedded.

We used the presence-absence model to predict posterior distributions of species richness and community-weighted mean traits for each of the scenarios.

2.7. Species richness analyses

To examine if those 55 rare species (with less than five occurrences) omitted from the HMSC analyses showed markedly different responses than the 64 common species (with five or more occurrences) included in the HMSC analyses, we performed complementary analyses of species richness. To do so, we applied Poisson regression with the R-package lme4, using the same fixed and random effects as for the HMSC analyses described above. We fitted the species richness models separately for the common species and for the rare species.

3. Results

3.1. Description of the data and patterns of species richness

The data contained in total 43,896 individuals of 148 species occupying 320 host trees. Out of these, 43,654 individuals belonged to those 64 species that occurred on at least five host trees. Among these

Table 1
Descriptions of the scenario simulations.

Scenario	Description
N0. Natural forest landscape, baseline	Natural forest landscape (Vienansalo region). The density of host trees was set to mean in Vienansalo for recently dead pines (2.3 per ha) and for previously dead pines (44 per ha). The 100 host trees were randomly chosen from the Vienansalo data (with resampling).
N1. Small host tree	As N0 but host-tree diameters were set to the smallest value in the Vienansalo data (DBH 15 cm).
N2. Large host tree	As N0 but host-tree diameters were set to the smallest value (DBH 44 cm) not covered by host trees in managed forest stands.
N3. Recently dead host	As N0 but time of death of all host trees was assumed to have taken place less than one year ago.
N4. Previously dead host	As N0 but time of death of all host trees was assumed to have taken place more than two years ago.
N5. Managed landscape	As N0 but we assumed a region with long forest-use history (Pirkanmaa).
M0. Managed forest, baseline	(Managed) forest in a region with short forest-use history (Kuhmo). The density of host trees was set to mean in managed forests in Kuhmo for recently dead pines (0.5 per ha) and for previously dead pines (4.2 per ha). The 100 host trees were randomly chosen from the managed forests data in Kuhmo (with resampling).
M1. High host tree density	As M0 but the density of dead host trees was set to the mean in natural forests in Kuhmo (1.3 and 28 per hectare for recently and previously dead host trees, respectively).
M2. Long forest-use history	As M0 but we assumed a landscape with long forest-use history (Pirkanmaa).

Table 2

Results of the Poisson regression models on species richness. In these analyses, all continuous predictors were scaled to zero mean and unit variance. For the categorical variable time since death, the reference level is class 1. For the categorical variable region, the reference level is Kuhmo. Significant results ($p < 0.05$) are highlighted by bold font.

Predictor	Common species		Rare species	
	Estimate	p-value	Estimate	p-value
Density of recently dead pines	0.0249	0.452	0.0228	0.829
Density of previously dead pines	0.0597	0.0951	−0.171	0.167
Trunk diameter	0.0368	0.0616	0.131	0.123
<i>Tomicus piniperda</i> galleries	0.0383	0.0383	−0.092	0.306
<i>Tomicus minor</i> galleries	0.0280	0.138	0.0262	0.780
Time since death (class 2)	−0.303	< 0.001	0.0766	0.707
Time since death (class 3)	−0.522	< 0.001	0.593	0.003
Region (Pirkanmaa)	−0.0736	0.216	0.518	0.011
Region (Viena)	−0.177	0.0170	−0.296	0.291

species, the mean (standard deviation) number of species per host tree was 10.7 (4.3), and the mean (standard deviation) number of individuals per host tree was 136.4 (139.4).

The species richness of common species was highest for host trees that had died less than year ago, whereas the species richness of rare species was highest for host trees that had died between two and three years ago (Table 2). The common species had highest species richness in Kuhmo region whereas the rare species had highest species richness in Pirkanmaa region (Table 2).

3.2. Model fit

The average (over species) explanatory power of the presence-absence part of the HMSC model was 0.81 (in the units of AUC) and its predictive power was 0.69 based on cross-validation. The average (over species) explanatory power of the abundance (conditional on presence) part of the HMSC model was 0.28 (in units of R^2) and its predictive power was 0.05 based on cross-validation. As the predictive power of the abundance (conditional on presence) model was almost negligible, we do not examine the results from the abundance model any further, and thus we focus below solely on the presence-absence model.

3.3. Parameter estimates

Variation in species occurrences were mainly explained by tree-level characteristics, as they accounted on average (over the species) for 63% of the explained variation. Out of this, more than half (35%) was attributed to the numbers of *Tomicus* galleries, the remaining part (28%) being attributed to the host-tree diameter and time-since death. The stand-level fixed effects (densities of recently and previously dead host trees) accounted for 13%, the stand-level random effect (forest stand) for 8%, and the landscape-level fixed effect (study region) for 16% of the variation.

Fig. 2 reflects the results of the variance partitioning by illustrating that the characteristics of the host tree influenced the majority of the study species. Most species preferred recently dead pines: the occurrence probability was highest in trees that died less than a year ago for 34 species and lowest for 15 species, making species richness decrease with time since death (Fig. 3). The number of galleries made by *Tomicus piniperda* affected positively the occurrence of 12 species and negatively 11 species (Fig. 2, Table S3). Species that favoured host trees with *T. piniperda* galleries were all well-known associates of primary bark beetles (such as *Placusa depressa*, *Rhizophagus depressus*, *Cylistr lineare*, *Thanosimus formicarius*; see e.g. Kenis et al., 2004), whereas species that avoided host trees with *T. piniperda* galleries included species associated with decomposer fungi and later decay stages (e.g. *Tetratoma ancora*, *Corticaria polypori*, *Enicmus rugosus*). The number of galleries of *T. minor*

affected positively 10 and negatively 19 species. Species favouring or disfavouring trees with *T. minor* galleries showed similar though less clear patterns than those observed for *T. piniperda*. The diameter of the host tree did not influence most of the species in a statistically supported manner (Fig. 2).

At the stand-level, the density of the host trees and especially previously dead host trees had a predominantly positive influence (Fig. 2), making species richness increase with it (Fig. 3). Compared to the baseline level of Kuhmo, the species responded predominantly negatively to the study region being either Pirkanmaa or Vienansalo (Fig. 2), making species richness to be highest in Kuhmo (Fig. 3).

The amount of variation in the species' responses to the environmental covariates that was to a moderate extent explained by the measured traits ($R^2 = 28\%$, average over the covariates). The phylogenetic signal of the species' responses to environmental variation was high, the posterior mean (95% credible interval) of the parameter ρ being 0.81 (0.50, 0.99). This suggests the existence of traits that are correlated with the taxonomy and that influence species' responses to the covariates but that were missing from the present analyses.

3.4. Variation of species communities in the scenario simulations

Reflecting the result that the majority of the species preferred recently dead host trees, the species richness was lower in the scenario N4 of previously dead host trees compared to the baseline scenario (Table 3). Other than this, none of the scenarios showed a statistically supported difference compared to the baseline scenario in terms of species richness (Table 3).

Many of the scenarios differed from the baseline in terms of the species' traits. In particular, the scenarios N5 (natural forest in managed landscape) and M0 (baseline managed forest) differed from the baseline scenario of natural forest (N0) in a consistent way: the natural forest had a higher proportion of specialist species (in terms of total niche width and higher proportion of species specialized to conifers), a higher proportion of species preferring large host trees and little decayed host trees, and a lower proportion of species that are able to utilize logging residues, cut stumps and fallen trees (Fig. 4). Compared to the scenario M0 of the managed forest being located in a landscape with short forest-use history, even more specialist species were lost if the forest was located in a landscape with long forest-use history (M2) (Fig. 4).

The scenarios relating to the sizes of the host trees (N1 and N2) did not influence any of the traits (Fig. 4). The scenarios N3 and N4 related to the time since the host tree death showed expectedly that stands hosting recently dead pines contained a high proportion of species preferring early decay stages, and that stands hosting previously dead pines contained a high proportion of species specialized to pines (Table 2).

Average body size was the only species' trait that was not affected by any of the scenarios (Table 2). However, the variation in body size appeared to increase along with time since death of the tree (Fig. 3D).

4. Discussion

In this study, we asked how habitat availability and habitat quality at three spatial scales (host tree, forest stand, and landscape) influence saproxylic beetle assemblages, and particularly in relation to forest management. Out of these three scales, we found the scale of the host tree to be the most important, as the properties of the host tree explained more than half of the variation in the data. Particularly influential variables were the numbers of galleries of the two *Tomicus* species, which clearly indicates a priority effect of these early-arriving species on the species assemblages colonizing the trees later as was expected. In contrast, resource availability at the stand level, i.e. the density of recently and previously dead host trees, as well as the study region, had only relatively minor influences in our results. It is important to note that this does not at all mean that forest stands or

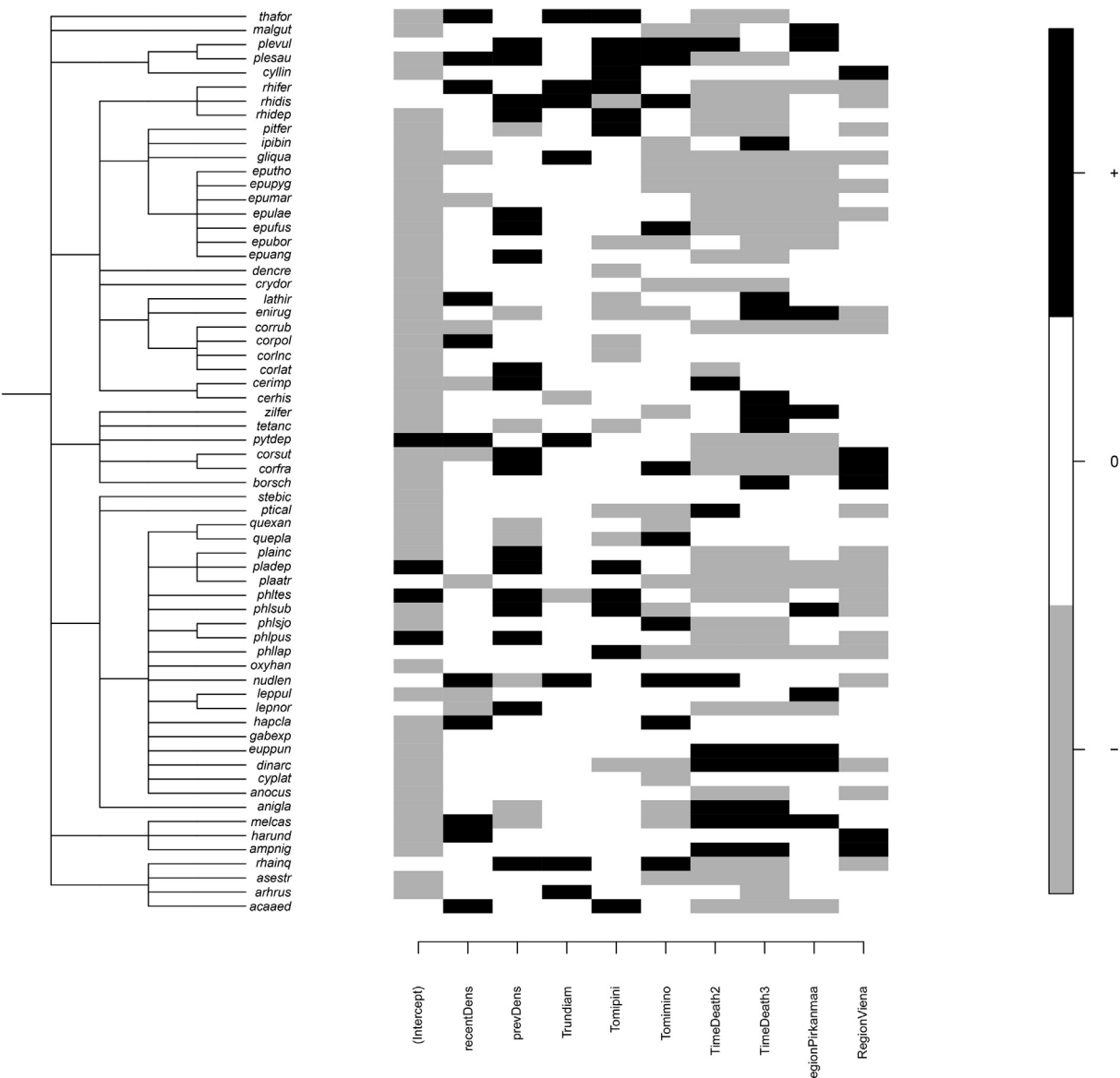


Fig. 2. Heatmap of estimated regression parameters measuring the responses of the species to environmental covariates. The species are organized as the rows and ordered according to their taxonomy, whereas the covariates are organized as the columns. The black and the grey colors show parameters that are estimated to be positive and negative, respectively, with at least 0.9 posterior probability in presence-absence model. For the abbreviations of the species' names, see Table S2. For the same information in numerical format, see Table S3.

landscapes with low densities of host trees would be equally valuable for conserving saproxylic species communities than forest stands or landscapes with high densities of host trees. This is because we analyzed the data at the host-tree level rather than forest-stand or regional levels, and because in our scenario simulations we standardized the amount of host trees when comparing the beetle assemblages that can be expected to be found under different environmental conditions. Thus, we asked how the properties of e.g. the forest stand influence the saproxylic beetle community inhabiting an individual host tree. At the forest stand level, the total population size is the sum over the available host trees and thus dependent on their density. We furthermore note that our results are not fully conclusive at the landscape level, as our study contained only three replicates at this level.

Our findings concur with previous reviews concluding that traits reflecting high habitat specificity can make species sensitive to habitat loss and fragmentation (Henle et al., 2004; Keinath et al., 2017). We found a higher proportion of specialized species in the saproxylic beetle community in natural forest landscape than in landscapes composed

mainly of managed forests. An average species had ca. 0.5 smaller total niche width in Vienansalo than in Pirkanmaa natural forests. This can be exemplified e.g. by every second species in a community using one dead-wood type less in the natural landscape compared to species communities in the managed landscape. Sverdrup-Thygeson et al. (2017) compared responses of specialist and generalist veteran-oak-dwelling species to different levels of habitat connectivity. They found, similarly to us, that specialists were more sensitive to disrupting connectivity between habitat patches. The possible mechanisms giving disadvantage for habitat specialists is that they experience more variation in habitat availability than generalists in managed landscapes (Miller et al., 2015), in the present case because the managed landscapes include low mean habitat availability of dead standing pines while at the same time cut stumps and logging residues are created by forestry measures at a constant rate. Variation in habitat availability elevates demographic stochasticity and decreases specialist species' long-term population growth rate (Lande et al., 2003; Ramiadantsoa et al., 2018).

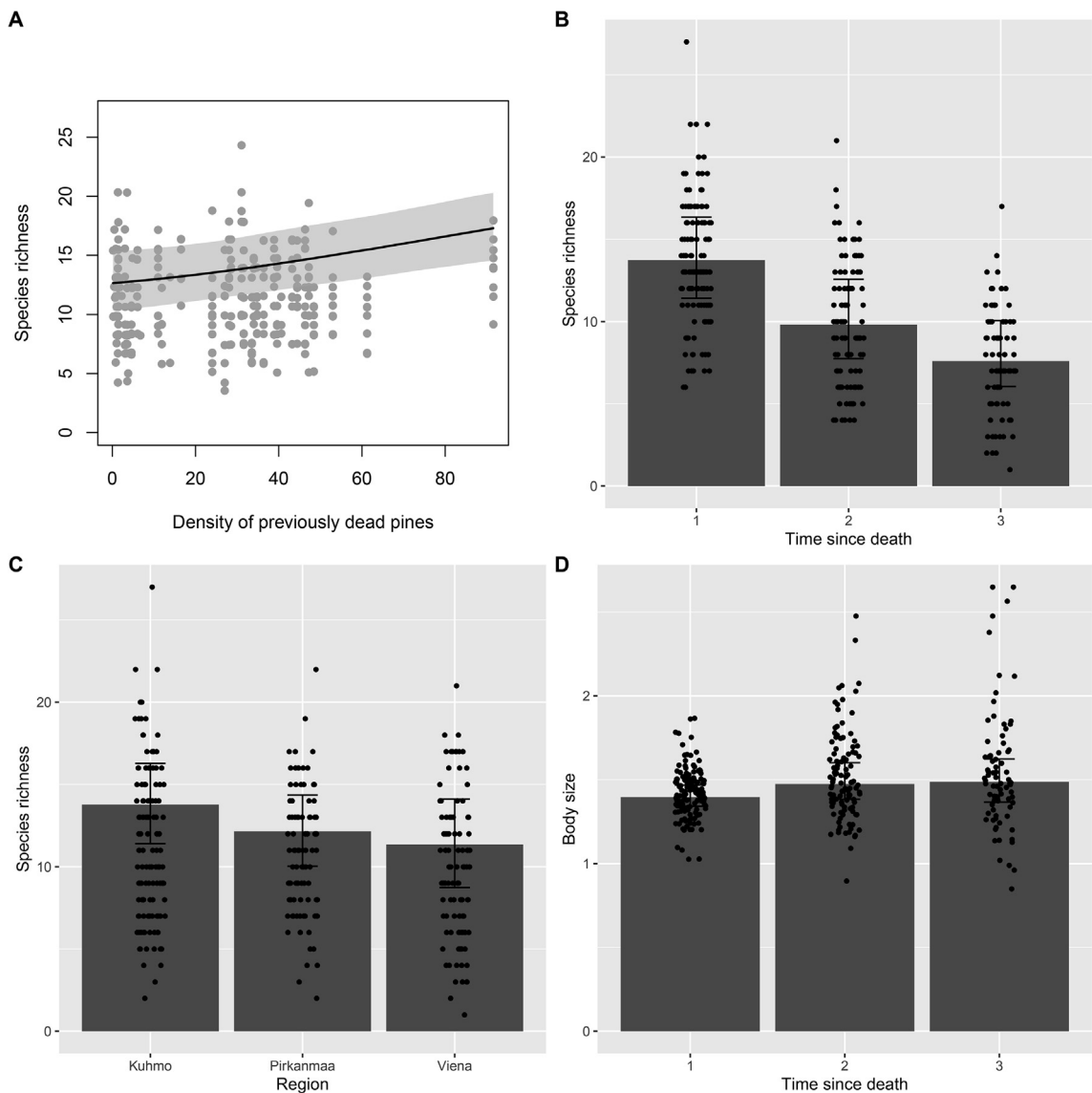


Fig. 3. Gradient plots of model predicted expected species richness and community-weighted mean of body size. The panels A–C show species richness as a function of the density of previously dead pines (A), the time since death of the host tree (B), and the study region (C). Panel D shows community-weighted mean body size (log-transformed length of the body) as a function of time since death of the host tree (D). All panels show the data and the mean and 95% credible interval of the model prediction.

Table 3
Influence of the simulated scenarios on species richness and community-weighted mean traits. All results are shown as comparison to the baseline scenarios (N0 and M0). The results are reported as ++ (P > 0.99), + (P > 0.90), – (P < 0.10), -- (P < 0.01), where P is the posterior probability by which the species richness or community-weighted mean trait is larger in the focal scenario than in the baseline scenario.

Focal scenario – Baseline scenario	Body size	Diameter niche	Decay niche	Tree-species specificity			Host-tree quality			Total niche width	Species richness
				Pine	Conifers	Coniferous and deciduous trees	Fallen trees	Cut stumps	Logging residue		
N1-N0											
N2-N0											
N3-N0			–	–	+		+				
N4-N0			+	+							–
N5-N0		–	+		–	++		++	++	++	
M0-N0		–	+	–	–	++	+	++	+	++	
M1-M0			–			–					
M2-M0			+		–	+		+		+	

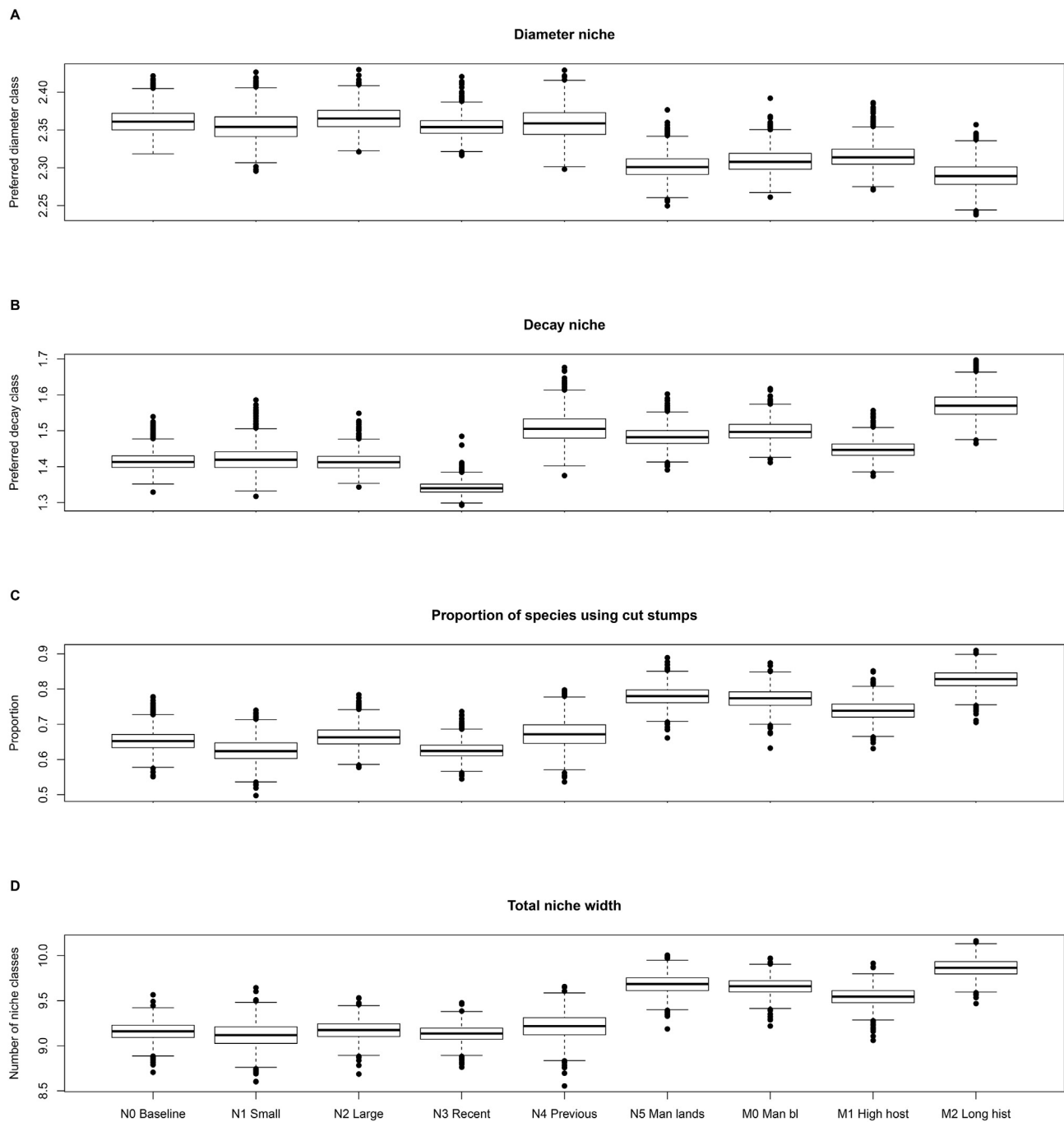


Fig. 4. Predicted distributions of traits among scenario simulations. The panels show the diameter niche (A), the decay niche (B), the proportion species of using cut stumps (C) and the total niche width (D). All panels show the community-weighted mean trait, the boxes show the median and 0.25 and 0.75 percentiles, and the whiskers the 0.025 and 0.975 percentiles.

Contrary to our expectations, we did not find body size to influence the vulnerability of saproxylic beetle species to forest-use intensity. This may be the case because all trunks included in our study were relatively large (DBH > 15 cm), and thus they were all perhaps sufficiently large to host also large-bodied species. There was, however, an indication of increasing body size variation along with dead-wood decomposition at the early stages of decay. Gossner et al. (2013) noticed an increase in mean body size and in body-size diversity of saproxylic beetles when the amount of dead wood and the mean dead-wood diameter increased. Janssen et al. (2017) got similar results, suggesting that the increase in body-size diversity is due to increasing heterogeneity of dead wood. Gibb et al. (2018) found a global trend of homogenization of body size

in ants, both smallest and largest species being absent from disturbed habitats. The potential decrease in body-size diversity of saproxylic beetles as response to diminishing quantities of dead wood and habitat heterogeneity deserves further attention.

We found the species richness to be higher in the landscape with short management history (Kuhmo) than in the natural landscape (Vienansalo). This perhaps unexpected result was partly explained by the fact that Kuhmo region had still preserved most of the specialist species while forest management had increased the number of generalist species benefitting from availability of cut stumps and logging residues. Furthermore, a larger proportion of study trees belonged to the age classes 2 or 3 in the Vienansalo region than in Finland. The

predominant mode of disturbance in pine-dominated natural forests in Fennoscandia is low-intensity surface fires, which lead to partial mortality and cohort dynamics (Kuuluvainen and Aakala, 2011). Autogenic mortality of individual trees or small groups of trees is also common, resulting in continuous recruitment of dead standing pines and a more or less uniform age distribution of such trees at the landscape level (Rouvinen et al., 2002; Kuuluvainen et al., 2017). The decreasing trend of species richness along with decay succession has also been observed in other studies on coniferous snags (Boulanger and Sirois, 2007; Saint-Germain et al., 2007). While it can be generally expected that saproxylic beetles preferring large trees and advanced decay stages are endangered in managed temperate and boreal forests (Seibold et al., 2015), in our study the assemblages consisted of secondary phloem feeders and their accompanying species in recently dead pines, and thus species preferring more decayed wood were not present in the data. Furthermore, it is important to note again that our results are per host tree rather than per forest stand, and that the natural landscape contained the highest density of host trees, including recently dead ones.

Summing over all of our results, we conclude that forest management not only reduces the amount of particular resources for saproxylic beetles locally, but has further landscape-level effects so that the most vulnerable species with specialized resource use and short-lived substrates can be lost also from remnant natural forest patches embedded in managed landscapes.

CRediT authorship contribution statement

Mervi Laaksonen: Conceptualization, Methodology, Writing - original draft. **Pekka Punttila:** Data curation, Writing - review & editing. **Juha Siitonen:** Data curation, Investigation, Writing - original draft. **Otto Ovaskainen:** Methodology, Writing - original draft.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary material

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.foreco.2020.118300>.

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